The role of kinship in field interactions among juvenile gray squirrels (*Sciurus carolinensis*)

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Received May 15, 1992
Accepted August 10, 1992

KOPROWSKI, J. L. 1993. The role of kinship in field interactions among juvenile gray squirrels (*Sciurus carolinensis*). Can. J. Zool. 71: 224–226.

Adult eastern gray squirrels influence recruitment into local populations by directing aggression at juveniles and nonresidents. However, the role of juveniles in the social dynamics of squirrel populations is poorly understood. Field interactions among juvenile squirrels were studied between littermates and nonlittermates. Amicable interactions occurred only between littermates, while aggression was directed almost exclusively at nonlittermates. Juveniles within their own natal areas dominated nonresident juveniles. Interactions among juveniles appear to be influenced by kinship and may be important in determining recruitment patterns in squirrel populations.

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Les Écureuils gris adultes agissent sur le recrutement des populations locales en étant agressifs à l'égard des juvéniles et des individus non résidents. Cependant, le rôle des jeunes dans la dynamique sociale des populations d'écureuils est mal connue. Les interactions entre les juvéniles ont été étudiées en nature, entre individus d'une même portée et entre individus de portées différentes. Les interactions amicales ne se produisaient qu'entre individus d'une même portée, alors que les interactions agressives se produisaient presque exclusivement à l'égard des juvéniles non apparentés. À l'intérieur de leur territoire natal, les juvéniles résidents dominaient les juvéniles non résidents. Les interactions entre juvéniles semblent dépendre du lien de parenté entre eux et influencent probablement les patterns de recrutement au sein des populations d'écureuils.
[Traduit par la rédaction]

Introduction

Social behaviour can be an important population regulatory mechanism among the squirrels (Mammalia: Sciuridae) (Armitage 1986; Thompson 1978*a*, 1978*b*). Aggression frequently is directed toward ingressing, nonresident individuals (Thompson 1978*a*, 1978*b*). Populations may demonstrate significant substructure in kinship when kin groups form as a result of natal philopatry (Armitage 1987; Koprowski 1991*a*). Kinship can be influential in recruitment of individuals and the distribution of aggression. Closely related kin receive less aggression than more distantly related and unrelated individuals (Armitage 1987; Koprowski 1991*a*; Sherman 1981) and close kin tend to share space and recruit into populations near their natal areas (Armitage 1987; Koprowski 1991*a*; Thompson 1978*b*). Adults are often considered to be of greatest consequence to behavioural regulation of recruitment because immatures are subordinate to adults (Allen and Aspey 1986).

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Printed in Canada / Imprimé au Canada

However, juveniles may remain near the natal area and also can have a vested interest in deterring recruitment of other cohort members.

Some juvenile eastern gray squirrels (*Sciurus carolinensis*) remain in their natal area; natal philopatry can be female-biased (Cordes and Barkalow 1972; Koprowski 1991*a*) or unbiased by sex (Thompson 1978*b*). Kinship significantly influences the apportioning of aggressive and amicable behaviour among adult gray squirrels, with closely related kin treated preferentially (Koprowski 1991*a*). However, do related and unrelated juveniles treat each other differently in field encounters? The objectives of this study were to determine if kinship influences the outcome of juvenile interactions and to examine whether the sexes differ in interaction rates.

Study area and methods

The study area was a 4.2-ha black walnut (*Juglans nigra*) dominated parkland located on the University of Kansas campus, Lawrence. From May 1986 to May 1990, squirrels were livetrapped, ear-tagged with numbered tags, and freeze-marked for permanent identification at a distance. A detailed description of the study area and methods is presented in Koprowski (1991*b*). During summer 1988, the spring-born litters (comprised of 7 males and 14 females) of 7 resident adult females were monitored from 1 June to 15 August (3.5–6 months of age), the period immediately post weaning. Maternity was easily determined for juveniles because females den with and nurse their litters in isolation (Nixon et al. 1975); spatial overlap between litters was less than 10% in this study. However, paternity could not be determined because females mate with several males (Koprowski 1991*a*). Therefore, relatedness of individuals was based upon maternal genealogy. I scanned the area with 7–15 × 35-mm binoculars while walking a standardized route at 20-min intervals during 210.5 h of observation focused during peak periods of activity (6:00–11:00 and 17:00–21:00); interactions were recorded *ad libitum*. The absence of a shrub stratum and the habituation of squirrels to humans facilitated observation. Each squirrel was identified and its location on a 6 × 6 m grid overlay recorded.

Amicable interactions included (*i*) allogroom: licking, mouthing, and grooming of another squirrel's pelage with the forepaws; (*ii*) greet: oral–nasal contact between two squirrels; and (*iii*) play: amicable wrestling between individuals. Agonistic behaviours included (*i*) chase: one individual chases another, frequently accompanied by tooth-chattering and barking; and (*ii*) aggressive contact: a continuum of behaviours from swatting with the forepaws to wrestling and biting. The individual amicable and agonistic behaviours were combined for analyses of the two general classes of behaviour. Frequencies of interactions were compared using χ^2 techniques, with expected values derived from the population composition of related–unrelated and same sex – mixed sex dyads. Home ranges were constructed as minimum convex polygons after removal of the outermost 10% of all locations, which represented forays to distant trees in fruit. Means ± 1 SD are presented in the text

Results

I observed 79 instances of amicable behaviour (0.38 interactions/h of observation) and 43 instances of agonistic behaviour (0.20 interactions/h of observation). Amicable behaviours were directed exclusively at littermates, while juveniles directed agonistic behaviour (98.7% of 43 agonistic encounters) at non-littermates. The eventual winner of the agonistic encounter usually initiated the interaction (42 of 43 agonistic encounters). Juveniles were similar in age (range of mother's day of estrus = 5 days) and weight (range = 40 g; 308.9 ± 14.5 g in late May – early June); therefore, individuals were likely at similar developmental stages and differences in size and experience likely did not account for differences in interlitter interactions. Sex was not a determinant of dominance; females chased males in 69.2% of 13 male–female agonistic interactions, which is similar to the sex composition of the population of juveniles (66.7% females; $\chi^2 = 0.04$; $P > 0.50$). However, most agonistic interactions (58.1% of 43 interactions) occurred when juveniles forayed from their home range, usually to forage in a tree with ripening fruit. Residents, which initiated all agonistic encounters, dominated nonresidents on forays in 96.0% of 25 agonistic encounters. Repeated agonistic interactions among juveniles were too infrequent ($n = 2$) to allow dominance interactions to be examined further.

TABLE 1. The observed and expected distributions of amicable and agonistic interactions among same- and different-sex dyads of juvenile eastern gray squirrels

Sex dyad	Frequency of interactions	
	Observed	Expected
Amicable interactions*		
Male–male	7	5.6
Male–female	42	33.9
Female–female	30	39.5
Agonistic interactions†		
Male–Male	12	4.4
Male–female	13	19.9
Female–female	18	17.8

*$P > 0.10$
†$P < 0.001$.

The number of amicable interactions were independent of the composition of sex dyads among littermates; the sexes interacted amicably in proportion to their abundance in the population (Table 1; $\chi^2 = 4.55$, $P > 0.10$). However, agonistic behaviour clearly differed between the sex dyads ($\chi^2 = 15.62$; $P > 0.001$); male–male chases were more frequent than expected, while juvenile males and females chased each other less often than expected. Agonistic encounters among females occurred as frequently as expected. Differences in interactions likely were not due to sex differences in home-range size or observability. Home ranges were similar between juvenile males (0.92 ± 0.61 ha) and females (0.84 ± 0.31 ha; $t = 0.40$, df = 19, $P > 0.50$). Similarly, males and females were observed equally often (34.83 ± 13.20 vs. 37.17 ± 18.30 observations/individual; $t = -0.29$, df = 19, $P > 0.50$).

Discussion

Interactions among juvenile gray squirrels were influenced by kinship, with aggression directed at unrelated individuals. The pattern of kin-directed amicable behaviour is similar to that observed among adult sciurids (Armitage 1987), including eastern gray squirrels (Koprowski 1991*a*). The ability to distinguish between related and unrelated juveniles appears to occur early in life. Kin discrimination in several ground squirrels (*Spermophilus beldingi*, *S. parryii*, *S. tridecemlineatus*) appears to depend in large part on familiarity (Holmes and Sherman 1982; Homes 1984). While the functional pattern of differential treatment of related and unrelated individuals is apparent, the mechanism of kin discrimination in eastern gray squirrels is unknown. Because females raise litters in seclusion (Nixon et al. 1975), spatial distribution and familiarity (reviewed by Holmes 1984) alone could account for the kin discrimination observed in field studies of this species (Koprowski 1991*a*).

However, future studies must experimentally determine the exact mechanism of kin discrimination.

Resident animals usually dominate nonresidents in a diverse array of taxa (Piper and Wiley 1989; Cristol et al. 1990 and references in both of these works). Although adults usually dominate juveniles, prior residence by juveniles can reverse the widespread phenomenon of age-related dominance (Cristol et al. 1990; Holberton et al. 1990). The tendency for resident dominance also occurs among sexually immature, juvenile gray squirrels in a field setting.

Natal philopatry is female-biased in my study area, with >95% of males dispersing from their natal areas (Koprowski 1991*a*), a pattern common among mammals (Greenwood 1980). Because females tend to be philopatric, females might be expected to interact most frequently, as in many female-bonded primate groups (Wrangham 1980). Amicable interactions were distributed evenly among sex dyads of gray squirrels; however, males were observed to aggressively chase each other more frequently than expected and females chased each other as frequently as expected. The sex differences that appear in natal dispersal after 6–9 months of age (Cordes and Barkalow 1972; Thompson 1978*b*) are not apparent in the levels of interaction among juveniles.

Although adult squirrels are important in the regulation of recruitment into a local population by directing aggression at immatures (Boutin and Schweiger 1988; Downhower and Armitage 1981; Thompson 1978*a*, 1978*b*), interactions among juveniles may also be of significance in determining recruitment patterns. Juvenile red squirrels (*Tamiasciurus hudsonicus*) fight with other juveniles when attempting to establish a territory (Boutin and Schweiger 1988). The most aggressive juvenile gray squirrels tend to establish residence, while less aggressive individuals disperse, even when all adult residents are removed (Pasitschniak-Arts and Bendell 1990). If dispersal results in significant fitness costs, juveniles can have a vested interest in establishing residence and, therefore, in defending their natal area. The process of kin discrimination and differential treatment appear to occur soon after weaning in eastern gray squirrels. Such social interactions may have considerable significance in determining recruitment patterns in the Sciuridae.

Acknowledgements

I thank three anonymous reviewers for helpful comments on the manuscript. I am grateful to the Theodore Roosevelt Memorial Fund of the American Museum of Natural History, Sigma Xi, The Scientific Research Society, and the Department of Systematics and Ecology at the University of Kansas for financial assistance. The University of Kansas Museum of Natural History graciously provided equipment. A Summer Fellowship from The Graduate School at the University of Kansas facilitated fieldwork. I also greatly appreciate the assistance of N. M. Koprowski in trapping and marking squirrels.

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